Three new species of the marine littoral mite *Hyadesia* (*Parahyadesia*) (Astigmata: Hyadesiidae) from southern Africa

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The marine mite family Hyadesiidae (Astigmata) comprises two genera (*Hyadesia* and *Amhyadesia*) with about 40 species worldwide. The taxon is restricted to littoral/supralittoral zones, having no true terrestrial representation. Collections from across southern Africa, from Elandsbaai on the west coast to Inhambane (Mozambique) on the east coast, contained three species each of *Hyadesia* Mégnin, 1891, and *Amhyadesia* Fain & Ganning, 1979. The present paper describes three new *Hyadesia* species, which belong to the subgenus *Parahyadesia* hitherto recorded only from New Zealand and containing four species. Distributions of two of the southern African *Hyadesia* (*Parahyadesia*) species overlap on the warm temperate to tropical southeast coast, whereas the third species is restricted to the cold temperate west coast.

Key words: Acari, acarofauna, marine mites, taxonomy.

INTRODUCTION

Mites of the family Hyadesiidae (Halbert 1915) are restricted to the marine littoral zones of the world, especially the rocky shores and the upper shorelines. They differ from the closely related Algophagidae (Fain 1974) in having, in particular, a long flexible pre-tarsus terminating in a claw on legs I and II (see Luxton 1989). Other differences and the phylogenetic relationship of these families are discussed in OConnor and Moser (1985). The Hyadesiidae contains two genera, *Hyadesia* Mégnin, 1891, and *Amhyadesia* Fain & Ganning, 1979, and about 40 species, most of which have been described by Fain and co-workers (Fain 1974, 1981; Fain & Ganning 1979; Fain & Schuster 1984, 1985, 1986) and Luxton (1989). The genera are distinguishable by their integumental characters: the dorsal integument of *Amhyadesia* is punctate or pitted, whereas that of *Hyadesia* is smooth (Luxton 1989). Three subgenera have been established for *Hyadesia,* namely, *Hyadesiella, Hyadesia* and *Parahyadesia* (Luxton 1989).

Algal scrapings and extractions from barnacles on rocky-shores across southern Africa (Fig. 1), from Elandsbaai (on the west coast; 32°20′S, 18°30′E) to Inhambane, Mozambique (on the east coast; 23°51′S, 35°29′E), contained both *Amhyadesia* and *Hyadesia* (*Parahyadesia*) spp. The current paper describes three new species of *Hyadesia* (*Parahyadesia*). Three *Amhyadesia* species are considered elsewhere (Marshall & Nunkumar 1999).

MATERIALS & METHODS

Fine algal turf from the upper rocky-shore *Littorina* zone (see Branch & Branch 1981 for zonation descriptions) was collected from numerous localities along the southern African coastline (Fig. 1). Some collections were also made from lower Balanoid algae and barnacles at Sardinia Bay (near Port Elizabeth) and Lwandile (Transkei). Specimens were preserved in 70 % ethanol. *Hyadesia* mites were sorted under a dissecting microscope, cleared in 70 % lactic acid at 60 °C for four days, slide-mounted in Hoyer's medium, and examined using phase contrast light microscopy (LM). More than 100 slides were prepared, with the best preparations designated as type material. Scanning electron microscopy (SEM) was undertaken to investigate the integument of some mites. Specimens were dehydrated in an ethanol series from 70 to 100 % (70, 80, 90 and 100 %), critical-point dried, mounted on stubs with double-sided tape and gold sputter-coated. Although more than one notation has been proposed for the idiosomal chaetotaxy of the Astigmata, we follow the initial and subsequent descriptions of the genus and species (Fain & Ganning 1979; Luxton 1989). All measurements are given in microns (μm).

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RESULTS

Three new species of *Hyadesia* are recorded from the coastline between Elandsbaai and Port Edward: *H. (P.) benguelensis* from Elandsbaai and Sea Point, *H. (P.) heteromorpha* from Mossel Bay, Brenton, Port Alfred and Port Edward, and *H. (P.) agulhensis* from Sardinia Bay (near Port Elizabeth) and Lwandile (Transkei) (Fig. 1). On the basis of a ventral process on femur II, which is especially conspicuous in the heteromorphic forms, all three species are referred to *Parahyadesia*.

***Hyadesia (Parahyadesia) benguelensis* n.sp.**, Figs 2, 3, 6

Material examined. In excess of 200 specimens, from green algal turf in the *Littorina* zone, Sea Point and Elandsbaai in July 1997.

Type material. Holotype: female, Sea Point, 06.vii.97; length 475, width 350 (Ref. no. 3C). Five paratypes: Sea Point, 06.vii.97; two nominate males 437 and 427 long, 275 and 295 broad (Ref. nos 1C and 1B, respectively); heteromorphic males 485 and 450 long, 325 and 287 broad (Ref. nos 2C and 2B, respectively); female 450 long, 302 broad (Ref. no. 3A). A single paratype of each sex and form will be deposited in the National Museum, Bloemfontein, South Africa.

Dorsum. Light microscopy showed a fine irregular patterning of integument over entire dorsum, similar to the ventral wrinkling described for *Hyadesia* (*Parahyadesia*) *tesselata* (Luxton 1989; Figs 2a). SEM showed this pattern to comprise fine pitting (Fig. 6c). Transverse dorsal folds or furrows sometimes visible, including an incomplete anterior dorsosejugal furrow, equidistant between *d1* and *sci* setae, and other furrows located level with setae *d2* and *d3*. Lateral surface oil grooves extend posteriorly from dorsosejugal furrow, between lateral and dorsal setae. Lateral branches of oil groove, anterior to *d2* and *d3* setal bases, terminate at pores. (The reference to pores is based on the use of this term in other papers describing *Hyadesia*. More correctly, they are tension sensory cupules found throughout the Oribatida and Astigmata). Opisthosomal oil glands conspicuous, opening into lateral grooves between setae *d3* and *l3*. Posterior to *d3* setae, lateral grooves branch to form a reticulate network, which gives rise to two pairs of lateral pores between the bases of *l4* and *d5* setae. Variation in reticulation complexity between individuals is considerable. Dorsal propodosomal shield (sclerite) punctate, longer than broad, tapering posterior of marginal propodosomal pores, and extending posterior to external scapular setae (*sce*).

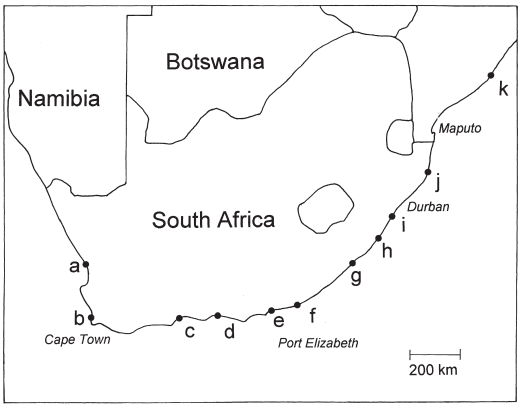

Fig. 1. Collection sites along the southern African coastline. **a**, Elandsbaai (West coast); **b**, Sea Point, Cape Town (West coast); **c**, Mossel Bay (southern Cape); **d**, Brenton (near Knysna, southern Cape); **e**, Sardinia Bay (near Port Elizabeth, eastern Cape); **f**, Port Alfred (eastern Cape); **g**, Lwandile (near Pressley Bay, Transkei coast); **h**, Port Edward (Kwazulu-Natal (KZN) south coast); **i**, Park Rynie (KZN, south coast); **j**, Mapelane (KZN, Zululand coast); **k**, Tofo (near Inhambane, Mozambique).

Dorsal chaetotaxy (Table 1, Fig. 2) conforms with that of other *Hyadesia* (*Parahyadesia*) species. Vertical setae (*vi*), which arise from vertex of shield, are smooth (see Table 1 for idiosomal setal lengths). External scapular setae (*sce*) typically long, broad-based and distally hooked. Internal scapular setae (*sci*) more than a third the length of *sce* setae. Five pairs of dorsal (*d*) series setae: *d1* short, curved, with a terminal flagellum; *d2*, *d3* and *d4* setae of similar length and more than twice that of *d1* setae; *d5* short, rigid and blunt. Five pairs of lateral setae: *l5* (bases ventral) typically long and distally hooked. The single pair of humeral (*h*) setae hooked at tips.

Venter. Dorsal integument patterning extends to ventral surface posterior to genital opening and is overlain with coarser, wrinkled lines radiating towards anal opening (not illustrated in Fig. 2b). Two pairs of genital setae (*ga* and *gp*) and one pair of anal setae (*a3*). *gp* setae longer than *ga* setae and with a terminal flagellum. Anal setae (*a3*) located at anterior end of anal fissure, relatively long and distally hooked. Apodemata I and II fused in male (Fig. 3), but discrete in female (Fig. 2). Apodemata III and IV fused in both sexes. Epigynium absent in female. Chitinous band surrounds anterior part of

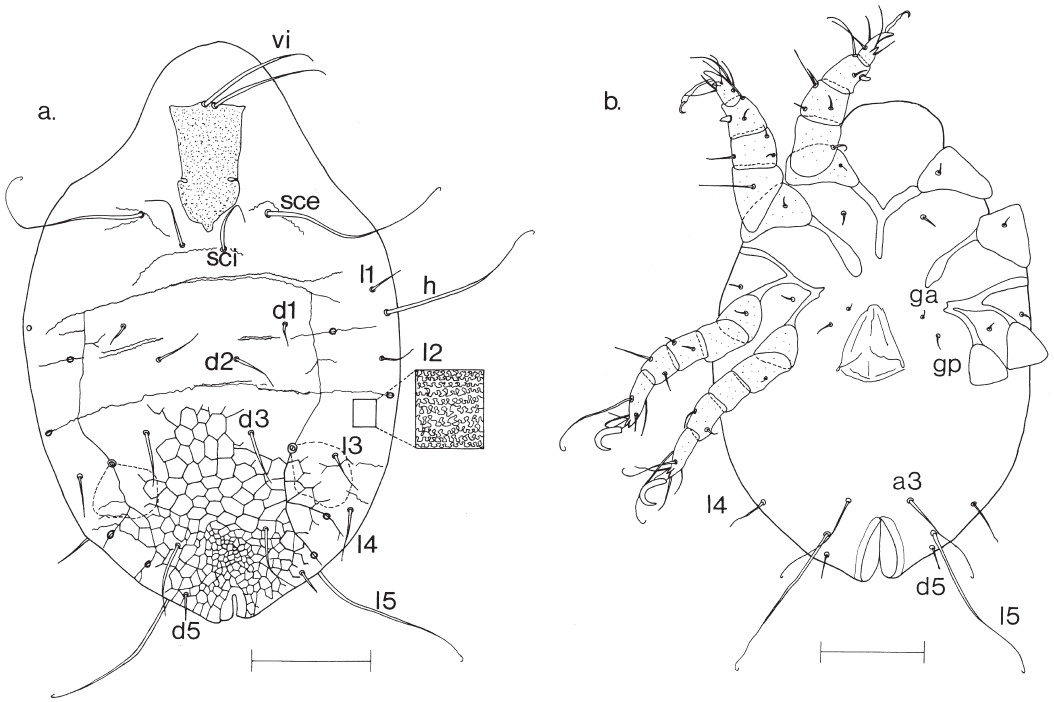

Fig. 2. *Hyadesia* (*Parahyadesia*) *benguelensis* n.sp.: **a**, dorsal female, scale bar = 100 µm; **b**, ventral female, scale bar = 100 µm.

male genital opening.

Legs. Typical of genus. Leg segments lengths given in Table 2. Integument sclerotized and pitted, though with soft integument sometimes conspicuous on distoventral surfaces of tibiae. In males: suckers on tarsi I, III and IV not always conspicuous (see Fig. 3), seta on femur II arises from a ventral process, which is particularly prominent in heteromorph. Setation (including solenidia) (coxa, trochanter, femur, genu, tibia, tarsus): leg I, 1,1,1,4 (2 with common base), 3 (ventral seta spiniform), 7 (plus 1 or 2 spines); leg II, 0,1,1 (seta terminal of ventral process in male), 3,3 (ventral seta spiniform), 6/7/8 (plus two spines); leg III, 1,1,0,2,2,5 (plus two spines); leg IV, 0,0,1,0,2,5 (plus two spines).

Etymology. The name is derived from the distribution of this species along the west coast of southern Africa, a region largely influenced by the cold, north-bound Benguela current.

***Hyadesia (Parahyadesia) heteromorpha* n.sp.**, Figs 4, 5

Material examined: In excess of 300 specimens from Port Alfred, Brenton Beach (near Knysna) and Mossel Bay. All material was collected from the *Littorina* zone, amongst finely-branched algal tufts, in June/July 1997.

Type material. Holotype: female, Brenton, 30.vi.97; 475 long, 350 broad (Ref. no. 3B). Five paratypes: Brenton, 30.vii.97; two nominate males 442 and 405 long, 270 and 260 broad (Ref. nos 1A and 1B respectively); heteromorphic males 505 and 490 long; 350 and 325 broad (Ref. nos 2C and 2B respectively); female 450 long, 312 broad (Ref. no. 3C). A single paratype of each sex and form will be deposited in the National Museum, Bloemfontein, South Africa.

Dorsum. Smooth with variable creasing, and transverse folding. Fine dorsolateral transverse lines extend ventrally (see Fig. 4). LM-observed lines not visible in SEM, therefore sub-surface features. Pattern of oil grooves and pores similar to that of *H*. (*Parahyadesia*) *benguelensis* n.sp., and possibly typical for the group. Surface lateral oil grooves extend posterior to anterior (incomplete dorsosejugal) furrow, branching laterally to pores posterior to *l1* and *l2* setae. Oil glands open into these lateral grooves between setae *d3* and *l3*. The grooves do not form a posterior reticulate network, but rather give rise to simple branches posterior to *l3* setae, each leading to an external

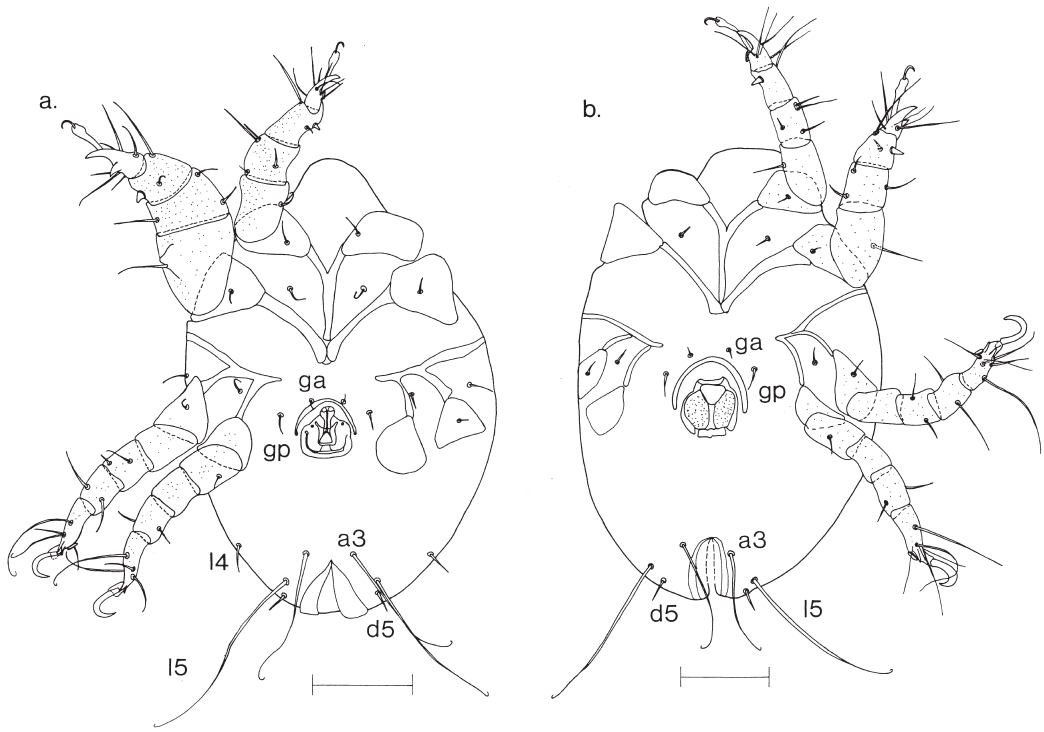

Fig. 3. *Hyadesia* (*Parahyadesia*) *benguelensis* n.sp.: **a**, ventral heteromorphic male, scale bar = 100 µm; **b**, ventral normal male, scale bar = 80 µm.

pore between setae *l4* and *d4*. Propodosomal shield rectangular, tending to being broader than long. It is weakly sclerotized and often indistinct, extending just beyond vertical oil pores, which are also sometimes indistinct.

Dorsal chaetotaxy (Table 1, Fig. 4): vertical setae (*vi*) arise from vertex of shield, fine and smooth. External scapular setae (*sce*) typically long, broad-based, distally hooked. Internal scapular setae (*sci*) approximately one-third length of *sce*. Five pairs of dorsal setae: *d1*, *d2* and *d3* similar in length, *d4* nearly twice as long, *d5* thin and short. Five pairs of lateral setae: *l5* typically long and distally hooked. One pair of humeral setae (*h*) with distal hooks.

Venter. May be patterned with fine straight lines as seen on dorsolateral surfaces (Fig. 4). Two pairs of genital setae, *gp* longer than *ga*, one pair of anal setae located at anterior end of anal fissure. Apodemata I and II fused in male, discrete in female; apodemata III and IV fused in both sexes. Small epigynium present in female. Genital plate well sclerotized and pitted in males.

Legs. Typical of genus; segment lengths given in Table 2. Integument sclerotized and pitted, with soft integument sometimes conspicuous on distoventral surfaces of tibiae. In males (see Fig. 5): suckers on tarsi I, III, and IV; single bifid spine at base of pretarsi III and IV; seta of femur II arises from a prominent ventral process, which is particularly conspicuous in heteromorphic males; ventral seta on trochanter III spiniform and associated with a process. Setation (including solenidia) of coxa, trochanter, femur, genu, tibia, tarsus: leg I, 1,1,1,3/4 (2 with common base; Fig. 5b), 3 (ventral seta spiniform), 8 (plus one or two spines); leg II, 0,1,1 (seta terminal of ventral process in male), 3,3 (ventral seta spiniform), 6/7/8 (plus two spines); leg III, 1,1 (spiniform in male), 0,2,2,6 plus two spines in female (five setae plus distal bifid spine in male); leg IV, 0,0,0,0,2,6 plus two spines in female (five setae plus distal bifid spine in male).

Etymology. The name refers to the spectacular heteromorphic males of this species.

***Hyadesia (Parahyadesia) agulhensis* n.sp.**, Fig. 6

Material examined. In excess of 60 specimens from Lwandile (Transkei) and Sardinia Bay (Port Elizabeth), collected from algal turf and barnacles in

Table 1. Body setal measurements (µm) of nominate male (n/mle) and female (fmle) types of the three species of *Hyadesia* (*Parahyadesia*), including the range for a further two females and five males including heteromorphs.

	H.(P). benguelensis			*H.(P). heteromorpha*			*H.(P). agulhensis*		
	n/mle	fmle	range	n/mle	fmle	range	n/mle	fmle	range
vi	107	97	92–117	75	120	75–120	95	102	95–112
sce	155	155	130–182	125	160	115–165	157	150	132–165
sci	55	45	45–70	45	52	45–67	55	42	32–55
d1	27	17	17–27	37	45	37–45	20	15	15–22
d2	50	50	50–62	32	52	32–52	45	50	42–50
d3	55	52	42–67	40	50	40–50	45	47	35–55
d4	57	55	57–77	60	90	60–90	52	52	32–65
d5	17	20	17–25	16	17	15–17	15	20	15–20
l1	45	37	30–45	32	35	32–52	32	27	25–35
l2	32	27	25–35	22	32	22–37	25	25	25–27
l3	35	32	32–42	32	32	27–35	30	30	27–40
l4	35	35	35–52	32	40	32–40	22	27	22–27
l5	150	162	150–200	187	237	162–237	170	140	142–170
a3	85	87	85–142	62	47	47–65	80	80	62–80
h	145	132	132–172	145	212	145–212	140	135	107–147

Table 2. Measurements (µm) of leg segments of the three species of *Hyadesia* (*Parahyadesia*) (l/w: length/width; n/mle, h/mle and fmle indicate nominate male, heteromorphic male and female, respectively; bold indicates measurement exceeding that of both of the other two forms for the species by ten or more units).

	H.(P). agulhensis			*H.(P). heteromorpha*			*H.(P). benguelensis*		
	n/mle	h/mle	fmle	n/mle	h/mle	fmle	n/mle	h/mle	fmle
Leg I									
Troch (l/w)	37/62	40/65	**50**/47	55/50	55/62	60/57	60/40	**70/60**	52/45
Femur	62/37	65/42	52/42	65/45	**85**/52	65/45	62/37	70/**55**	60/35
Genu	45/40	47/30	40/40	50/40	**67**/50	47/42	42/32	47/**50**	40/25
Tibia	47/35	47/30	37/30	45/32	**62**/37	50/37	35/22	**52/35**	37/22
Tarsus	22/17	22/15	20/17	22/17	27/20	22/17	25/15	20/17	25/10
Leg II									
Trochanter	35/70	**57/82**	35/55	42/62	**67/92**	52/62	50/**60**	**87**/50	52/50
Femur	80/55	**90/75**	60/42	75/55	**102/92**	72/50	70/45	**97/82**	62/37
Genu	42/50	**55/67**	37/35	52/55	**62/87**	47/45	45/37	37/**77**	37/37
Tibia	37/40	**47/52**	35/30	40/37	57/**62**	50/40	25/37	**42/57**	32/22
Tarsus	27/20	30/22	17/15	20/20	**30/35**	20/22	12/17	**30/27**	20/15
Leg III									
Trochanter	47/**60**	50/45	42/42	37/42	**62**/52	52/47	55/35	62/**50**	50/32
Femur	50/35	50/35	40/32	52/32	**62**/45	52/40	52/30	60/**45**	42/22
Genu	40/35	37/30	32/30	37/32	**52**/37	42/37	37/25	40/**35**	35/20
Tibia	42/30	35/25	37/25	37/30	50/32	42/32	37/22	40/30	32/22
Tarsus	50/17	45/17	37/17	47/15	55/20	50/22	35/15	45/22	40/15
Leg IV									
Trochanter	40/37	45/37	37/35	40/42	52/50	52/50	50/35	55/47	47/35
Femur	50/35	50/37	47/35	52/32	65/42	60/37	50/27	57/**42**	50/25
Genu	37/35	37/32	32/35	40/27	50/40	45/37	35/27	45/**37**	32/20
Tibia	40/25	37/27	37/25	40/27	52/35	55/32	40/22	42/**32**	30/20
Tarsus	50/20	42/20	40/17	47/15	52/20	50/22	37/15	**47**/22	37/15

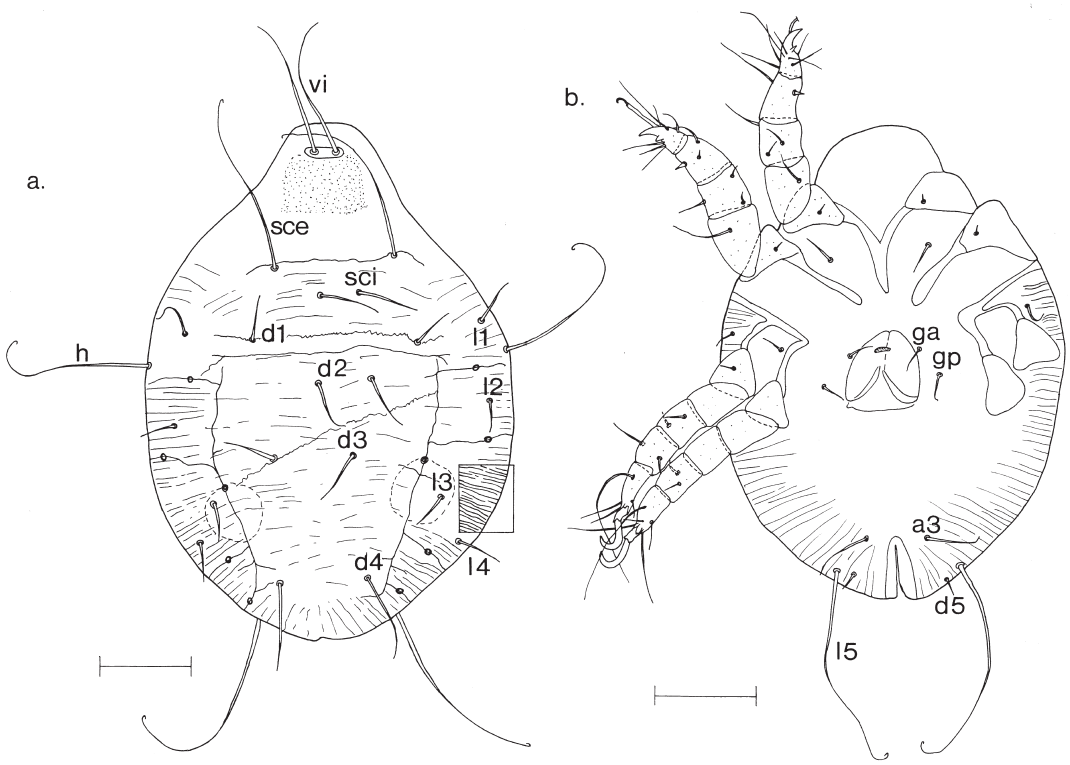

Fig. 4. *Hyadesia* (*Parahyadesia*) *heteromorpha* n.sp.: **a**, dorsal female, scale bar = 80 µm; **b**, ventral female, scale bar = 100 µm.

Littorina and balanoid zones.

Type material. Holotype: female, Lwandile, 24.xii.96; 475 long, 335 broad (Ref. no. 3A). Five paratypes: Lwandile, 24.xii.96; two nominate males 410 and 430 long, 275 and 297 broad (Ref. nos 1A and 1C respectively); two heteromorphic males 337 and 407 long, 262 and 275 broad (Ref. nos 2E and 2B respectively); female 450 long, 312 broad (Ref. no. 3B). A single paratype of each sex and form will be deposited in the National Museum, Bloemfontein, South Africa.

H. (P.) agulhensis is morphologically similar to *H. (P.) benguelensis.* Reference should thus be made to the description and figures of the latter species with regard to setal lengths and positions, oil glands and grooves, reticulation, and propodosomal shield. The species differ in particular by the absence of the fine integumental pitting in *H. (P.) agulhensis* (see Figs 2 and 6 for LM and SEM of integumental features of the species). *H. (P.) agulhensis* further differs from *H. (P.) benguelensis* in having relatively long *d5* setae, rigid *l4* setae, and shorter *a3* setae.

Etymology. The name reflects the distribution of this species along the east coast of southern Africa, which is influenced by the Agulhas current. The name also pairs the species with its sibling west coast species also named after a prominent oceanic current.

Heteromorphic males

Heteromorphic males are usually larger than nominate males, with idiosomal setae variable in length among males, in proportion to body size. Setae may be associated with processes. Heteromorphs are conspicuous by their larger legs, particularly leg II (Figs 3, 5; Table 2) in which most segments are relatively thicker and longer in all three species (Table 2). Other legs of heteromorphs are also relatively larger than those of the nominate forms in *H. (P.) benguelensis* and *H. (P.) heteromorpha* (see Table 2). The functional significance of the robust legs in the heteromorphic male of *Parahyadesia* is unknown, but possibly facilitates mating. In the terrestrial astigmatid mite, *Caloglyphus berlesei* (Acaridae), heteromorphic males fight and kill other males to achieve greater reproductive success (Radwan 1993).

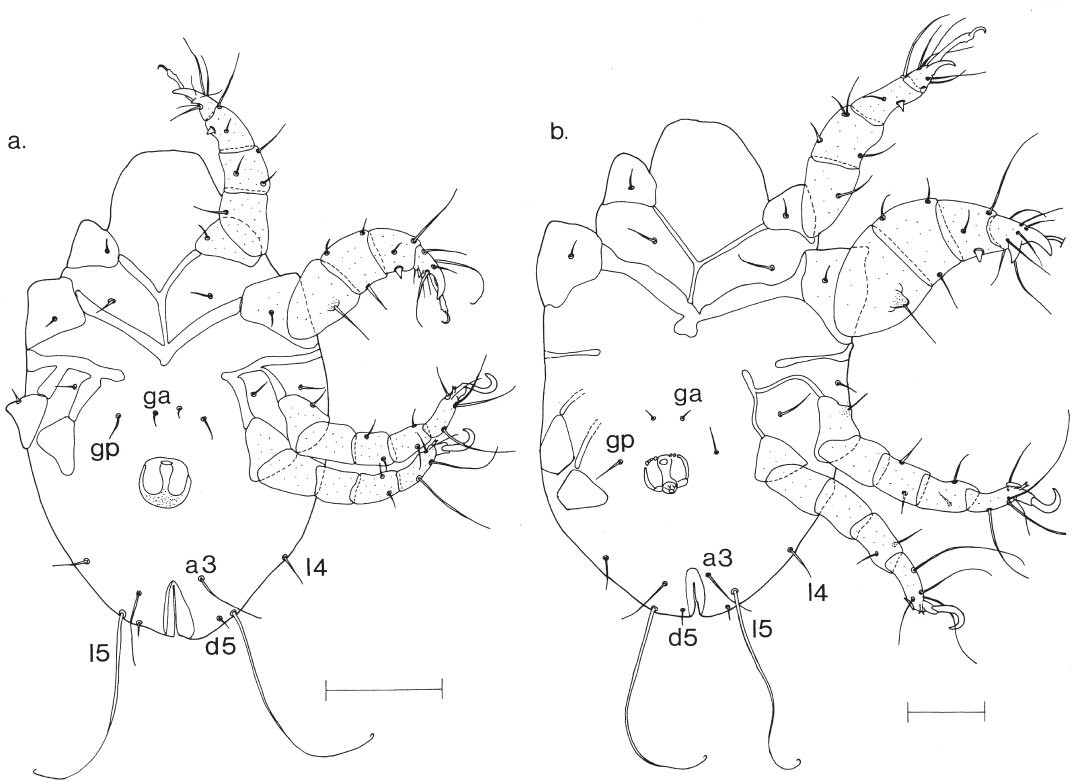

Fig. 5. *Hyadesia* (*Parahyadesia*) *heteromorpha* n.sp.: **a**, ventral normal male, scale bar = 100 µm; **b**, ventral heteromorphic male, scale bar = 80 µm.

DISCUSSION

All three species were adjudged as *Hyadesia* (*Parahyadesia*) on the basis of a prominent ventral process on femur II of the heteromorphic male (Luxton 1989). This subgenus has previously only been recorded as four species from New Zealand, *H.(P.) mollis, H.(P.) reticulata, H.(P.) plicata* and *H.(P.) tesselata* (Luxton 1989), suggesting a possible Gondwanan origin for these hyadesiid mites. The New Zealand and southern African species share numerous similarities, especially dorsal and ventral idiosomal setation. Collectively, the geographic taxa differ in some setal lengths, particularly the *sce*, *l5* and *a3*, which are consistently longer in the New Zealand species (see Luxton 1989).

There is, however, no consistent southern African versus New Zealand pattern, with regard to other idiosomal characters. For example, *H. (P.) heteromorpha* is closest to *H. (P.) mollis* in the shape of the propodosomal shield and the relative lengths of *d1* and *d2* setae. These species differ in integument features (no wrinkling in *H. (P.) mollis*) and *a3* setal lengths. Similarly, *H. (P.) benguelensis* and *H. (P.) agulhensis* share the reticulated integument seen in *H. (P.) plicata* and *H. (P.) reticulata*, but differ in many other respects. Leg and other non-idiosomal characters are most appropriate in grouping the species. *H. (P.) heteromorpha* and the New Zealand species, share a bifid spine at the base of male pretarsi III and IV, female epigynium, absence of femur IV seta, and the spinous seta projecting from a process on trochanter III of the heteromorph. The sibling southern African species, *H. (P.) benguelensis* and *H. (P.) agulhensis*, have simple spines on either side of the claw ambulacrum at the base of pretarsi III and IV, in place of the bifid spine, and differ from *heteromorpha* and the New Zealand species in the characters listed directly above.

Integument patterning of *H. (P.) benguelensis* as observed using LM (apparently similar to that in the New Zealand, *H. (P.) mollis*), was found to comprise fine surface pitting when viewed at higher magnification under SEM (Fig. 6). This has impli-

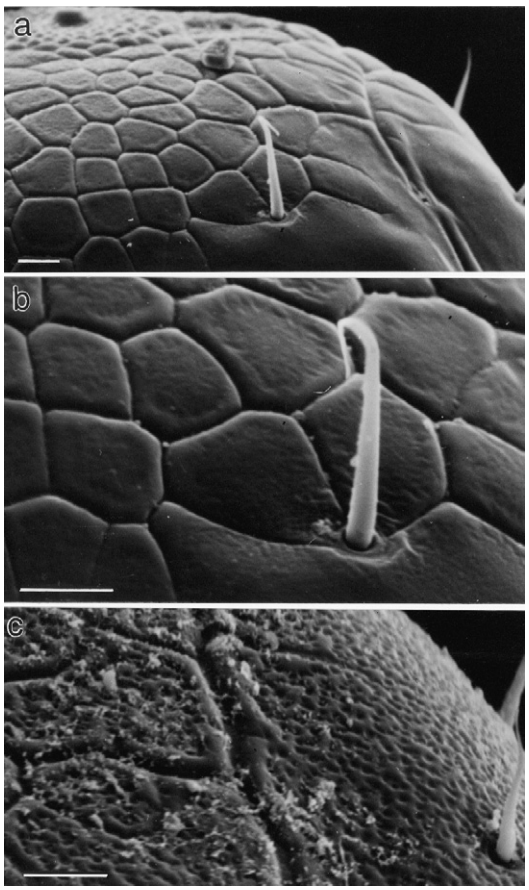

Fig. 6. Scanning electron micrographs of integument surfaces. **a**, Posterodorsal surface of *Hyadesia (P.) agulhensis* showing reticulation (*d4* seta in foreground); **b**, higher magnification of surface depicted in (a); **c**, posterolateral integument of *H. (P.) benguelensis*, showing edge of reticulation and pitting of the surface. All scale bars = 10 µm.

cations for hyadesiid taxonomy as pitting and/or punctation are used to differentiate *Hyadesia* (pitting absent) and *Amhyadesia* (pitting present) (Luxton 1989). Furthermore, pitting in *H. (P.) benguelensis* but not in *H. (P.) agulhensis* is used here to distinguish these closely-related species, both of which have reticulated posterior dorsal surfaces (Figs 2, 6). Clearly pitting/punctation and reticulation of the integument need to be revisited and redefined if they are to be used with confidence in future taxonomic studies on hyadesiid mites.

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REFERENCES

BRANCH, G. & BRANCH, M. 1981. *Living Shores of Southern Africa.* C. Struik Publishers, Cape Town.

FAIN, A. 1974. Acariens récoltés par le Dr. J. Travé aux îles subantarctiques. I. Families Saproglyphidae et Hyadesidae. *Acarologia* **16**: 684–708.

FAIN, A. 1981. Notes on the Hyadesiidae and Algophagidae, nov. tax. with a redescription of *Hyadesia curassaviensis* and *H. sellai*. *Acarologia* **22**: 47–61.

FAIN, A. & GANNING, B. 1979. *Amhyadesia californica*, g.n., sp.n. (Acari, Astigmata, Hyadesiidae) from the southern California coast. *International Journal of Acarology* **5**: 139–142.

FAIN, A. & SCHUSTER, R. 1984. Four new species of the genus *Amhyadesia* Fain & Ganning 1979 from the intertidal zone of several Indo-Pacific islands (Acari: Hyadesidae). *International Journal of Acarology* **10**: 103–111.

FAIN, A. & SCHUSTER, R. 1985. New observations on the Hyadesiidae description of three new species of the genus *Hyadesia*. *Acarologia* **26**: 67–77.

FAIN, A. & SCHUSTER, R. 1986. First record of the mite family Hyadesiidae from the Madeira Archipelago. *Bocagiana* **99**: 1–10 .

HALBERT, J.N. 1915. Acarinida: II. Terrestrial and marine Acarina. *Proceedings of the Royal Irish Academy* **31**: 45–136.

LUXTON, M. 1989. Mites of the family Hyadesiidae (Acari: Astigmata) from New Zealand. *Zoological Journal of the Linnean Society* **95**: 71–95.

MARSHALL, D.J. & NUNKUMAR, S. 1999. First records and descriptions of the marine littoral mite genus *Amhyadesia* Fain and Ganning, 1979 (Acari: Astigmata: Hyadesiidae) from southern Africa. *South African Journal of Zoology* **34**: 173–179.

MÉGNIN, P. 1891. Note sur un Acarien de la Terre de Feu (*Hyadesia unicifer* n.g., n. sp.). *Mission Scientifique du Cap Horn* 1882–1883, Paris, **6**.

OCONNOR, B.M. & MOSER J.C. 1985. Phylogenetic relationships of the Algophagidae (Acari: Astigmata), with descriptions of a new subfamily, genus and species. *Annals of the Entomological Society of America* **78**: 783–789.

RADWAN, J. 1993. The adaptive significance of male polymorphism in the acarid mite *Caloglyphus berlesei*. *Behavioural Ecology and Sociobiology* **33**: 201–208.